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A causal analysis of the relationships between behaviour patterns of free living warthogs

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Abstract

Studied were, using factor and concordance analysis, the causal relationships between behaviour patterns of free living warthogs *Phacochoerus aethiopicus* in the Andries Vosloo Kudu Reserve, Eastern Cape Province, South Africa. Warthog behaviour patterns fall into five categories with similar causal relationships, the first two broad categories consisting of social behaviours, a third large category comprising comfort behaviour patterns, the other two consisting of agonistic and feeding behaviour. Comparison of the number of factors necessary to explain over 80% of the behavioural variance in warthogs with those for other species indicates that warthogs have a behavioural repertoire based on less complex causal relationships than primates, social carnivores and dolphins but more complex than that of bovines.

Introduction

Knowledge of warthog *Phacochoerus aethiopicus* behaviour has increased during the last 30 years, with qualitative descriptions having been given for warthogs in different areas of Africa (see Radke 1991 for a review and Somers 1992 for the present study area). They are therefore not repeated here.

To determine the role of various behaviour patterns in the social life of animals it is important to analyse their causal relationships (Rasa 1977). Both factor and concordance analysis are useful means by which behaviour patterns can be classified into those with similar causal relationships or similar motivational backgrounds and their comparison provides checks on the validity of the groupings found (Van Hooff 1970). The logic behind these types of analyses, which are based on behavioural sequences, is that the closer one behaviour pattern is related to another, the greater the tendency that each of them would be followed by other behaviour patterns in the behavioural repertoire at similar frequencies. These transition frequencies would thus be expected to show close correlation with one another. Factor analysis of the correlation coefficients obtained then allows their grouping into categories with a high degree of relatedness between behaviour patterns, as indicated by their high loadings on a particular factor. The relationship of a behaviour pattern with its highest loading on any one factor to those of other groups is indicated by its next highest and subsequent loadings on other factors discriminated by the analysis (Frey and Pimental 1978).

In this study on the causal factors of warthog behaviour, the frequency with which each behaviour pattern followed another was determined by sequence analysis. Warthog

behaviour patterns have not previously been analysed as to their causal factors. Since they are social group living animals a complex behavioural structure was predicted, as described for primates (van Hooff 1970) and social mongooses (Rasa 1977; Wenhold 1990).

Material and methods

The study was conducted on the Andries Vosloo Kudu Reserve (AVKR) ca 40 km north-east of Grahamstown, Eastern Cape Province, South Africa, between 33×04′ and 33×09′ S, and 26×37′ and 26×49′ E. For a description of the study area and animals used see Somers et al. (1995).

The data were collected from the central part of AVKR, the majority within a 1.5 km radius of a homestead (Grasslands). Observations were made from a vehicle, which served as a hide, and occasionally on foot. The warthogs which lived near Grasslands homestead were habituated to the presence of vehicles before the study began. Thirteen females and 34 males were individually known over the duration of the study period (March 1989–December 1990). Binoculars (7×35) were used when necessary. Groups were observed from the time they exited the burrows in the morning to the time they retired in the afternoon or evening.

To determine general activity (see Somers et al. 1995) scan samples (Altmann 1974) were taken at 5 min intervals for all visible members of a group (n = 887 hours). All occurrences of some events sampling were used especially for social behaviour patterns, which have a short duration and are likely to be under-represented in scans (Martin and Bateson 1993). If these occurred within the period of the 5 min scans, they were recorded in sequence.

The methods used for the sequence analysis were as previously described by Rasa (1977). The behaviour patterns included in this analysis were: resting, eating, retreating, standing, running, drinking, wallowing, grooming, allogrooming, suckling, greeting, playing (including solitary and social play), approaching, threatening, fighting, exiting of burrows, entering of burrows, excavation of burrows, scent marking, sniffing, grunting, squealing, courting and copulating, a total of 24. Walking was not included as nearly all behaviour patterns were necessarily correlated with it (Slater and Ollason 1972). As qualitative descriptions have been given elsewhere (see Radke 1991), only the descriptive names of behaviour patterns are given here.

Since a behaviour pattern could precede itself by a warthog stopping a particular behaviour at one site, walking to another and resuming that behaviour, the diagonal of the transition matrix was potentially full. Expected frequencies could therefore be calculated and these were corrected for random variation using the eccentricity coefficient (o-e)/(e, where o = observed frequency and e = expected frequency (Van Hooff 1970).

The eccentricity coefficients were then ranked and a Spearman's rank correlation analysis performed on the matrix, a particular behaviour pattern being considered as most closely correlated with itself and thus allocated the correlation coefficient "1.0". To determine communality amongst the behaviour patterns, the correlation coefficients were subjected to factor analysis with varimax rotation as well as concordance analysis using the method described by McQuitty (1966).

In the factor analysis four factors were extracted, these explaining 84.4% of the variance of all the behaviour patterns under consideration. Two behaviour patterns which loaded negatively on all four factors were considered separately.

Results

The first column of the factor analysis (Tab. 1) shows the highest loadings for different behaviour patterns on the four factors that explain 84,4% of the variance in warthog behaviour, 45.4% being explained by Factor I, 18.3% by Factor II, 12.6% by Factor III and 8.1% by Factor IV. The next highest loadings and the factors on which these loadings fall are shown in columns II–IV.

Those behaviour patterns with their highest loadings on a particular factor are grouped together (A, B, Ç, D). A further group (E), consisting of the, behaviour patterns

Table 1. A component analysis of the structure of behaviour patterns of warthogs, given by component loading (multiplied by 100). F = factor, L = loading

	Loading:	I (highest)		II (Second)		III (Third)		IV (Fourth)	
	Behaviour	F	L	F	L	F	L	F	L
A	Approach	I	74.5	II	48.5	III	39.6	IV	16.3
	Suckle	I	63.3	II	59.6	III	7.2	IV	0.2
	Exit	I	89.5	II	25.7	III	19.4	IV	16.2
	Threat	I	81.8	II	36.7	IV	27	III	–20.4
	Copulate	I	90.4	II	24.1	IV	17.6	III	17.1
	Squeal	I	75.4	III	43.3	II	41.6	IV	11.7
B	Retreat	II	91.2	I	10.8	III	3.9	IV	–25.9
	Greet	II	88.1	I	36.3	III	–4.6	IV	–15.2
	Court	II	65.0	I	51.8	III	14.3	IV	–4.6
	Play	II	14.9	III	0.5	I	–28.2	IV	–82.2
	Mark	II	24.5	III	11.8	IV	–7.8	I	–66.7
	Sniff	II	85.1	III	22.6	IV	17.8	I	3.9
C	Excavate	III	66.1	I	33.3	II	32.1	IV	–25.7
	Run	III	66.8	I	65.2	II	11.7	IV	8.0
	Wallow	III	70.8	I	55.8	III	19.3	IV	–24.3
	Allogroom	III	32.8	II	30.6	I	–7.1	IV	–88.3
	Rest	III	76.8	II	20.7	II	–30.1	I	–44.2
	Grunt	III	58.0	IV	55.3	II	42.7	I	26.7
	Groom	III	82.7	IV	23.3	II	11.2	I	–0.01
D	Fight	IV	74.4	III	50.8	I	22.4	II	21.7
	Enter	IV	52.3	III	44.9	I	17.3	II	–4.5
	Drink	IV	70.8	III	16.7	II	–10.9	I	–50.5
E	Eat	IV	–14.9	III	–21.5	II	–25.5	I	–90.3
	Stand	III	–18.7	II	–24.6	I	–53.3	IV	–71.8

"eat" and "stand", had negative loadings on all 4 factors, indicating that further factors are necessary to explain the complete behavioural repertoire.

Behaviour patterns of Group A, except for exiting of burrows, are social, as are all the behaviours in Group B. Groups C and D contained only one behaviour where interaction between two individuals occurred, namely allogrooming and fighting respectively. Group C contained behaviour patterns which can be broadly categorised as comfort behaviour, those of Group E being associated with feeding. The behaviour patterns falling into Group D, however, appear to have no common causal basis.

To determine the closeness of relationship between different behaviour patterns and to act as a check on the groupings extracted from the factor analysis, a concordance analysis was conducted using the correlation coefficients obtained from the transition matrices. The results are shown in Figure 1, the higher the concordance coefficient, the closer the causal relationship between behavioural complexes.

Six main groups were found to be present. The first one, A, corresponded to the first group from the factor analysis but included, in addition, courting and eating. Group A was further subdivided into three subgroups, the first including suckling, exiting and eating. This subgroup appeared to be hunger related. The second subgroup consisted of squealing and approaching, these being associated with initiation of social contact and the third subgroup included courting and copulating, sexually orientated behaviours. Group B comprised the behaviour patterns excavation of burrows and wallowing while Group C in-

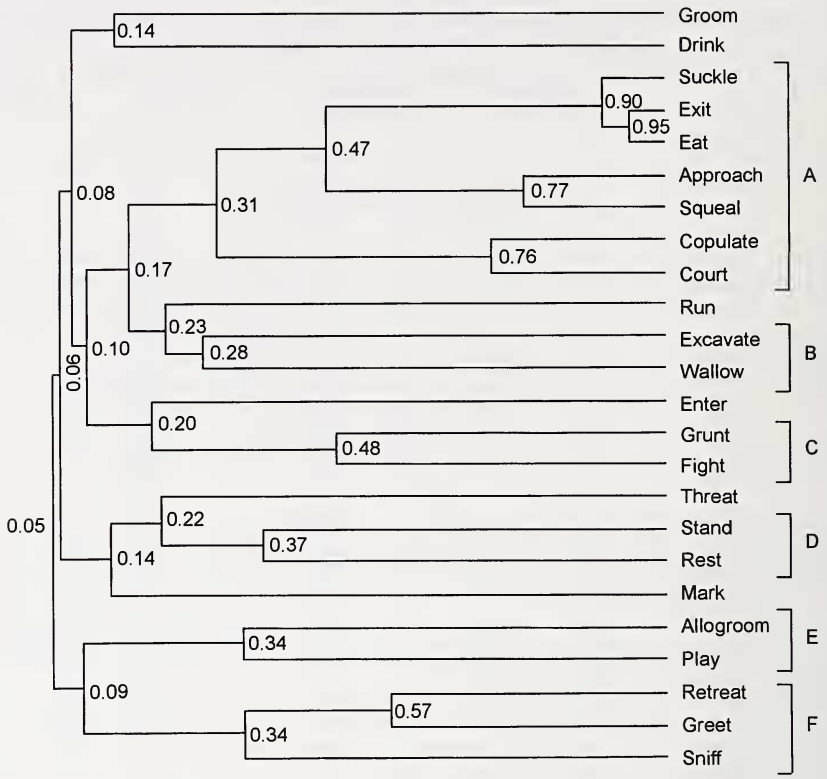

Fig. 1. Dendrogram of the relationships between behaviour patterns obtained through concordance analysis. The concordance coefficients are shown at the junction of the lines connecting the different behaviour patterns or behaviour pattern complexes.

cluded grunting and fighting, the latter being aggressive behaviour patterns. Group D consisted of standing and resting, both behaviours being associated with bodily inactivity. Group E contained allogrooming and play, behaviours occurring in a friendly social context while Group F was comprised of retreating, greeting and sniffing, these being associated with submissive behaviour.

The concordance analysis indicated that some behaviour patterns were not closely causally related to any others. The behaviour patterns concerned were grooming, drinking, running and entering of burrows, these being associated with body maintenance but causally unrelated. Threatening and marking, the other two behaviour patterns in this category, could both be loosely described as having an agonistic function.

Discussion

This study has shown that warthog behaviour can be subdivided into four main categories with a similar causal basis using factor analysis. Concordance analysis indicates that these relationships can be further subdivided into 8 categories with different motivational backgrounds, only 6 behaviour patterns showing no close causal association with any of the others. Five of these categories consist of behaviour patterns occurring in a social context, supporting the hypothesis that warthogs, being social, group-living animals, should show a high degree of behavioural complexity.

Of the subgroups with their highest loading on Factor I, those comprising Group B, burrow excavating and wallowing, are of especial interest since the findings suggest that burrow excavation has a function previously not recognised. During excavation, the soil is tossed into the air, covering the excavator and other warthogs in the vicinity. This may be a form of comfort behaviour, as is wallowing, soil being a protection against insolation and an aid in removing parasites, as in African elephants *Loxodonta africana* (Skinner and Smithers 1990). In the factor analysis wallowing and excavation of burrows have their highest loadings on the same factor as grooming and allogrooming, further supporting this hypothesis. The main function of burrow excavation was thought to be provision of a refuge for escape from predators (Bradley 1968, 1971; Cumming 1975; Radke 1985, 1991). Our data, however, indicate that it is more closely allied to comfort behaviour than to behaviour patterns associated with fleeing and escape or anti-predator behaviour (running, entering burrows or threatening).

Some groupings in both analyses may be explained by the fact that even if one activity always follows another, they may not be causally related to each other, but rather to some other factor (Staddon 1972). The results can be influenced by various factors such as the environment, and by individuals and groups differing (Slater and Ollason 1972). If the data from different animals are not combined, however, a massive quantity of data will have to be collected (Slater and Ollason 1972). These shortcomings in the data may explain the separation of behaviours which may otherwise be considered causally related. Entering and exiting burrows are weather and time dependent, entering occurring, for example, in the evenings and during the heat of the day. These external factors may have influenced both their factor loadings and concordance coefficients.

Van Hooff (1970) stated that, in sequence analyses, the less complex the behavioural structure, the smaller the number of components required to explain a large part (ca 70 to 80%) of the total variance. In warthogs, 84.4% of the variance was explained by only four factors, a fifth group being negatively loaded on these four. Comparison with other mammals indicates that 83% of behavioural variance is explained by 7 factors for chimpanzees, *Pan troglodytes* (Van Hooff 1970), 80% or more is explained by 11 factors for dwarf mongooses, *Helogale undulata* (Rasa 1977) and 81.5% is explained by 10 factors for yellow mongoose, *Cynictis penicillata* (Wenhold 1990). However, over 80% of the behaviour of captive silver (*Vulpes vulpes*) and blue (*Alopex lagopus*) foxes can be explained by 4 factors (Harri et al. 1995), by 5 for Hector's dolphin (*Cephalorhynchus hectori*), and only 3 for Holstein cows (de Passille et al. 1995). Warthog behavioural complexity therefore lies between that of the highly social primates and mongooses and the dolphins and at a level equivalent to foxes but above that of cattle.

Factor and concordance analyses are powerful tools for analysing causal relationships between behaviour patterns and are finding new application especially in the study of aberrant behaviour in domestic animals (Harri et al. 1995; de Passille et al. 1995). Probably owing to the difficulties inherent in conducting the analyses, those based on behavioural sequences are available only for a few species to date. This method of behavioural analysis, however, may also be useful in indicating phylogenetic relationships or levels of sociality for species, based on the number of factors necessary to explain behavioural variablity, as well as indicating causal relationships between behaviour patterns themselves.

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Zusammenfassung

Kausalanalyse der Beziehungen zwischen Verhaltensmustern freilebender Warzenschweine

Mittels Faktoren- und Konkordanzanalyse werden Kausalbeziehungen zwischen Verhaltensmustern freilebender Warzenschweine *Phacochoerus aethiopicus* im Andries-Vosloo-Kudureservat, Südafrika, untersucht. Die Ergebnisse weisen ein relativ unkompliziertes Verhaltensmuster auf. Die Aktivitäten sind allgemein in vier Gruppen verteilt, von denen soziale und andere Aktivitäten die zwei Hauptgruppen bilden.

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